
Effects of Constitutive and Inducible Traits of Hybrid Poplars on Forest Tent Caterpillar Feeding and Population Ecology

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ABSTRACT. Hybrid *Populus* spp. clones, differentially affected forest tent caterpillar, *Malacosoma disstria*, behavior, development, and population dynamics. Increased larval cohort size and larval silk generally enhanced development. Larval behavior affected developmental success. Under choice conditions, larvae selected more suitable clones, and their growth was enhanced when they moved from less to more suitable hosts. Herbivory by the forest tent caterpillar caused significant reductions in the quality of foliage for subsequent larval development. Polar and nonpolar foliar extracts varied between constitutive and previously damaged plants, and elicited significant larval behavioral responses. The extent to which prior feeding induced foliar changes that affected larval feeding and development varied among clones. The ability of forest tent caterpillar to exploit clones includes genetic and environmental components affecting foliar quality, and includes positive and negative density dependent feedback. In whole-tree field cages, forest tent caterpillar populations increased 9.7× during a 2 yr period on a highly suitable clone, and declined 2.7× on a poor quality clone. The relationships between clonal suitability and forest tent caterpillar population growth were strongly influenced by bud phenology and exudates, in addition to foliar traits. *For. Sci.* 43(2):252–267.

Additional Key Words: *Malacosoma disstria*, Lasiocampidae, *Populus* spp., feeding ecology, induction.

The success of insect folivores is affected by host physical and chemical traits, whose expression is regulated by genetic and environmental controls, and complicated by insect and plant life history characteristics and changes in host quality due to herbivory (Bowers 1992, Futuyma 1991, Haukioja 1990, Herms and Mattson 1992, Jones 1991, Simms and Fritz 1990). Understanding these interactions is confounded by difficulties in extrapolating from specific plant properties affecting insect success

under controlled conditions, to whole-plant interactions and population dynamics. In the current study, this variety of interactions was studied across a range of scales from laboratory studies of plant extracts to population dynamics over 2 field generations.

The forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae), is an early season, univoltine, oligophagous defoliator of deciduous trees throughout eastern North America (Drooz 1985, Fitzgerald 1995). Its eco-

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conomic importance and greatest ecological impact in north-central North America are primarily due to cyclical outbreaks which occur at 6 to 16 yr intervals and persist 2–6 yr (Batzer et al. 1995, Duncan and Hodson 1958, Hodson 1977). Native aspens, *Populus tremuloides* and *P. grandidentata*, are its primary hosts in this region (Rose 1958). Hybrid poplar, *Populus* spp., plantations are also at risk to this insect (Ostry et al. 1989, Robison and Raffa 1990).

The suitability of hybrid poplars for the forest tent caterpillar varies significantly among clones (Robison and Raffa 1994). Clonal variation can be exploited to reduce pest impacts by using resistant native clones, selecting for enhanced resistance, and using deployment strategies that adversely affect pests (Dickmann and Stuart 1983). Information on the modalities and mechanisms of host plant resistance is needed to fully develop these potentials (Bingaman and Hart 1992, 1993, Robison and Raffa 1994), but is not usually generated during traditional screening of clones (Abrahamson et al. 1990, Caldbeck et al. 1978, Dickmann 1978, Ostry and McNabb 1985, Wilson and Moore 1985, 1986).

The impact of the forest tent caterpillar on native aspens (Duncan and Hodson 1958, Rose 1958), and aspects of its nutritional ecology under laboratory conditions (Karowe 1989, Lindroth 1992, Lindroth and Bloomer 1991) have been studied. However, few studies have specifically addressed the impact of constitutive and induced host plant traits on the behavior and development of this insect (Hodson 1941, Smith et al. 1986). Among native poplars, foliar phenolic glycosides are known to affect a variety of insects (Bryant et al. 1987, Lindroth et al. 1986, Meyer and Montgomery 1987, Palo 1984), but little is known about the relationships between host plant quality and population dynamics, or the potential for herbivory to elicit foliar responses that affect insect behavior and development. In addition, the effects of within and between clone variation on feeding ecology, and the interactions between life history characteristics and foliar traits, have not been examined.

Robison and Raffa (1994) quantified the susceptibilities of 15 hybrid poplar clones to the forest tent caterpillar in glasshouse and laboratory studies. In the current study, 5 of these clones possessing a broad range of susceptibilities were selected for detailed evaluation. Additional aspects of the constitutive properties of these 5 clones, and subsequent verification of their relative susceptibilities, are reported fully in Robison (1993). In the current study, experiments were conducted to explore the relationships between behavior and development, and the effects of herbivory-induced changes on feeding ecology for these clones. Ecdysis phenology, dispersal, food choice, survival, and growth were evaluated. The effects of social facilitating factors, such as larval cohort size and silk, on behavior and development were also considered. Clonal differences in foliar quality and induction were evaluated based on larval responses to foliar extracts. Two clones were used to examine the linkages among laboratory, glasshouse, and field assays of plant resistance, and the impact of clonal differences on insect population growth in the field.

Methods

This study addressed questions in 5 areas of forest tent caterpillar feeding ecology: (1) How does constitutive variation in clonal suitability affect larval development, and to what extent can these differences be attributed to behavioral responses to bud and leaf characteristics? (2) How do social facilitating factors such as larval group size and larval silk affect host plant utilization? (3) How does prior feeding damage affect subsequent host plant suitability for larvae? (4) Can clonal differences in larval suitability be attributed to foliar toughness, moisture, nitrogen, and allelochemicals? (5) How do differences in clonal suitability identified in laboratory and glasshouse assays in this and previous studies (Robison 1993, Robison and Raffa 1994) relate to populations on field trees, and what life table parameters are most affected by these interactions?

Following a description of insect and tree culture, experiments are described in the following order: effects of constitutive clonal variation, silk and group size, foliar changes due to herbivory, and foliar extracts on larvae, and population dynamics on caged field trees.

Forest Tent Caterpillar and Hybrid Poplar Culture

Egg bands were collected in winter (1989–1990, 1990–1991) from outbreak populations on native aspens on the Menominee Indian Reservation (ca. N 45° 00', W 88° 45') and in Marinette County (ca. N 45° 15', W 87° 45'), Wisconsin, and kept frozen until use. Insects were reared from surface sterilized (6% NaHClO) eggs on artificial diet (Grisdale 1985) in 35 ml plastic cups with paper lids at 16:8 L:D, 22–24°C, and 45–55% RH. Larvae were transferred directly from artificial diet to experimental chambers, unless noted.

The poplar clones studied were: NC11004 (= Siouland), *Populus deltoides*; NC11382 (= NE27), *P. nigra* 'Charkowiensis' × *P. berolinensis*; NC11445 (= NE280 and NE157), *P. nigra* × *P. laurifolia*; NM6 (= MAX 5), *P. nigra* × *P. maximowiczii*; and NE332, *P. simonii* × *P. berolinensis*. *P. berolinensis* is a hybrid of *P. nigra* × *P. laurifolia*. Clones were established with frozen 12 cm long dormant hardwood cuttings in a shaded glasshouse at 16:8 L:D (supplemented with standard fluorescent lamps), which fluctuated seasonally between 18–35°C and 25–100% RH. Cuttings were planted in saturated Redi-Earth Peat-Lite (W.R. Grace and Co., Cambridge, MA) potting soil in 20 cm diameter plastic pots, or evenly spaced in 46 × 24 × 15 cm plastic trays. Trees were fertilized with 15 g/plant Osmocote (Sierra Chemical Co., Milpitas, CA) slow-release 17-6-12 plus micronutrients, and flood-irrigated regularly. Trees were actively growing, less than 1 yr old, and 25–50 cm tall, when assayed.

Field tests were conducted in a hybrid poplar plantation established in April 1988 on the University of Wisconsin-Madison Arlington Experiment Station, Columbia Co., WI (ca. N 43° 14', W 89° 24') (Robison and Raffa 1997). Trees had been planted in clonal blocks (4 trees/block), at 1.22 × 1.22 m spacing, replicated 12 times.

All experiments were standardized for leaf position. The most apical fully unfolded (nonexpanded) leaf was assigned as No. 1, and lower leaves were sequentially numbered down

each stem or branch. Constitutive plants had not been subjected to leaf removal or larval feeding. Plants on which larvae had fed (previously damaged) contained leaves which were chewed (directly damaged) or unchewed (systemically damaged).

Larval Responses to Constitutive Variation Among Clones

Effect of Bud Surface Characteristics on First-Instar Mobility

First-instar larvae were placed singly on sunlit buds on actively growing branch-tips of clones NC11382 and NE332 in the field and glasshouse. Larvae were placed on the portion of the bud immediately distal to the first leaf with a visible petiole. Larval ability to move from the buds after 30 min. and 24 hr in the glasshouse, and after 30 min. in the field, was recorded.

Expanding buds of field grown NC11382 and NE332 were excised immediately distal to the first leaf with a visible petiole. The distal 75% of all leaf tips were cut from the excised bud. Several buds from each clone were put immediately in 11 ml MEOH at ca. 26°C and extracted for 2.5 hr at -1.0°C. Cumulative length (± 0.1 mm) and oven-dry (65°C) weight (± 0.1 mg) of composite samples were recorded for each clone. The oven-dry (65°C) weight (± 0.1 mg) of the extracted material was determined from a 2 ml aliquot of each extract. Extracts, stored in darkness at -28°C, were separated in a reverse phase ODS column (4.6 mm inside diameter, 25 cm long, 5 μ m particles; Axxion Chroma., Inc.) on an isocratic, reciprocating pump LC-6A high performance liquid chromatograph (HPLC, Shimadzu, Inc.) with a Rheodyne injector, a 20 μ l sample loop, and a Shimadzu SPD-6A UV spectrophotometric detector with a D₂ lamp at 254 nm and a 10 mm cell path. The solvent system was 1:3 MEOH:H₂O at 1.8 ml/minute, and chart speed of 2 cm/min. Peak heights were standardized to 0.01 UV detector absorption.

Effects of Clonal Suitability on Early-Instar Movement

The dispersal behavior of newly enclosed L1 larvae from clones NC11004, NC11382, NM6, and NE332 was studied by suspending an egg band from an upper petiole of trees ($n = 5$ trees/clone each with 1 egg band). Trees were fitted around the base with a 30 \times 30 cm white plastic card coated with petroleum jelly. Larvae hatched and fed or dispersed freely. The number of larvae stuck to the cards were counted daily throughout the first stadium, and the total number of enclosed larvae per egg band was counted.

The effects of clonal deployment patterns on larval movement were simulated by dispensing egg bands into 2 planting designs ($n = 5$ for each design). Nine trees each of 1 highly preferred (NC11004) and 1 nonpreferred (NM6) clone were planted in plastic trays in the glasshouse. Trees were arranged in either uniform block or alternating mixed-tree patterns (Figure 1). NC11004 and NM6 trees were approximately 10 and 25 cm tall, respectively. An egg band was suspended from the top of a wooden dowel in each half of the trays (2 egg bands/tray) at canopy height (23 cm in NM6, 8 cm in NC11004, 15 cm in mixed clones). The feeding location of each colony (1 colony from each egg band) was recorded daily for 7 days (near 12:00 hr), through the 2nd-instar.

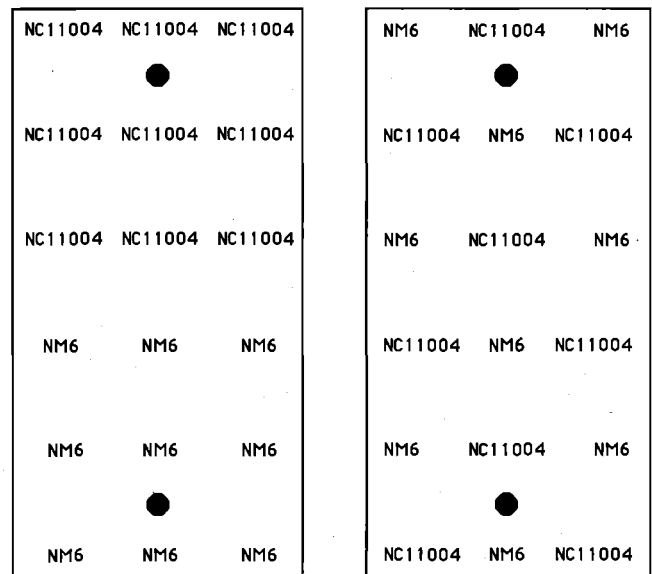


Figure 1. Planting designs of 2 hybrid poplar clones in 24 \times 46 cm trays in a glasshouse. Left side is "uniform" block, and right side is "mixed tree" plantings. • indicates the location of a forest tent caterpillar egg band.

Larval movement and feeding preference between clones was studied by pairing preferred and nonpreferred potted clones of similar height. Leaves from paired trees were intertwined and held together with twist-ties. The paired combinations were NC11382 and NE332 ($n = 8$), or NC11004 and NM6 ($n = 8$). One egg band was suspended between each pair in the upper third of the plants. Emerging larvae were allowed to feed and move freely until 2 days after each colony molted to the 3rd-instar (10–21 days). Total number of leaves/tree was recorded, individual leaf defoliation visually estimated ($\pm 5\%$), and defoliation/tree calculated (Σ defoliation/leaf + total number leaves/tree). A relative defoliation index (RD), ranging from 0 (no preference) to 1.0, was calculated for each pair to account for differences in total feeding among pairs: $RD = (\% \text{ defoliation preferred clone} - \% \text{ defoliation nonpreferred clone}) \div (\% \text{ defoliation preferred clone})$.

Leaves from these trees were also evaluated in an experiment on leaf choice, described in the next section.

Effect of Leaf Position on Early-Instar Feeding Preference

Choice tests were conducted in 15 cm diameter plastic petri dishes. The bottoms were coated with paraffin wax and covered with Whatman (Clifton, NJ) #50 filter paper moistened with distilled water. Leaf disks, 1.4 cm², were excised intervenally from NC11382 and NE332 field trees and anchored in the dishes with minuten pins. Single leaf disks from leaf positions 1, 2, 4, 6, 8, 10, 12, and 14 were positioned evenly around the circumference, within 1–4 mm of the dish walls. Six L2 larvae were introduced into the center of each dish, the dishes were covered and sealed with Parafilm (Greenwich, CT) tape, and the larvae were allowed to feed for 30 hr at 16:8 L:D, 24°C, and 100% RH. Consumption was measured with a LI-COR (Lincoln, NB) 3100 area meter.

Larval feeding preferences among leaves on whole-plants of NC11004, NC11382, NE332, and NM6 were assessed in the glasshouse. Feeding by young colonies was recorded on a per leaf basis during the previously described larval movement experiment which used paired trees.

Effects of Clonal Switching on Larval Development

The effects of combinations of high and low quality clones on larval development were evaluated. Larvae were fed 1 of 4 sequences of foliage: (1) clone NC11382 for 10 days, (2) NE332 for 10 days, (3) NC11382 for 5 days followed by NE332 for 5 days, or (4) NE332 for 5 days followed by NC11382 for 5 days. Assays were conducted in 6 × 6 × 21 cm clear plastic boxes lined with a paper towel at 16:8 L:D, 24°C, and 100% RH (12 boxes/clone, tops sealed with tape). Petioles of freshly cut glasshouse No. 4 leaves were inserted through Parafilm caps into vials containing distilled water, and placed in the boxes. Unfed L1 larvae (2-day-old) were put on the top surface of the leaf in each box. Ten larvae were put in half of the boxes, and 13 larvae were put in the remainder. In boxes with 10 larvae, new foliage from the same clone and leaf position was provided after the initial 5 days. In boxes with 13 larvae, 3 larvae were removed after the initial 5 days (for use in an experiment not reported here), and new foliage from NE332 was used to replace NC11382 foliage, or vice versa. Survival and group weight (± 0.1 mg) per box were recorded at 5 and 10 days.

Effects of Silk and Group Size on Larval Behavior and Development

The upper surface of an NC11445 leaf was coated with larval silk by herding 36 diet-reared L2 larvae on the leaf for 15 min. with a blunt probe. Herding encouraged walking and deposition of silk, but prevented feeding. Diet reared larvae ($n = 15$ L1 and $n = 15$ L2) were dropped individually from ca. 10 cm above the upper surface of a horizontally held silked or control leaf (from leaf positions 4 and 5). After 3 to 5 sec, the bottom of the leaf was firmly tapped twice with a blunt probe, and larvae were recorded as secure or dislodged. All larvae were dropped onto the same silked or control leaf, one after another. Confounding effects between subsequent larvae dropped on the same leaf were prevented by limiting assays to 3 to 5 sec, which prevented feeding and most walking.

Feeding was compared among varying larval densities on silked and unsilked leaves. Leaf petioles (positions 4 and 5) from glasshouse grown NC11004 were inserted through Parafilm caps on vials containing distilled water. Leaves were placed in 6 × 6 × 21 cm clear plastic boxes lined with paper towels, at 16:8 L:D, 24°C, 100% RH. Leaves were either untreated or coated with silk by herding 10 L3-L4 forest tent caterpillars on their top surfaces for 2–3 min. One, 2, 3, 5, or 10 unfed L1 larvae (1.5-day-old) were put on the center of each leaf's upper surface ($n = 5-9$), box tops were sealed with tape, and the larvae were allowed to feed for 6 days. Larval survival and group weight (± 0.1 mg) were recorded after 6 days. Consumption was measured by pressing the leaves under glass on Dri-print (Dietzgen, Inc.) paper to photographically develop images of the nonconsumed leaf

areas. Images were transferred to acetate and measured (LI-COR 3100 area meter), consumed regions of each leaf on acetate were filled with black ink, approximate total areas of the original leaves were measured, and areas consumed were calculated.

Larval Responses to Previously Damaged Clones

Effect of Prior Injury on Second-Instar

Feeding Preference

Leaf Nos. 4 and 5 on glasshouse clones NC11382, NE332, and NC11445 were enclosed in 10 × 12 cm white nylon screen (7 threads/cm) envelopes to prevent larval access and feeding. These screens do not significantly reduce photosynthetic activity (Krause 1994). Five trees per clone were infested with 0, 5, or 10 L3 larvae for 7 days. Larvae fed freely, but were confined to the plant by a band of petroleum jelly around each pot. Leaves in the screen envelopes on damaged (5 or 10 larvae) and constitutive (0 larvae) trees were used as systemically damaged and corresponding control leaves, respectively. Defoliation, estimated as described previously, ranged from 2% to 11%, 2% to 11%, and 2% to 20% among clones NC11382, NE332, and NC11445, respectively. Trees infested with 5 or 10 larvae were pooled, as defoliation did not differ between these groups.

The day after larval removal, 1.4 cm² intervenal leaf disks were excised in equal numbers from as many leaves (Nos. 3–8) as possible having the various treatments, and placed in 5 cm petri dishes as described previously for 2-choice preference assays. Three L2 larvae were put in the center of each dish, and the tops were sealed with tape (16:8 L:D, 24°C, 100% RH). Within-clone choice tests compared systemically damaged versus constitutive, and directly damaged versus constitutive, leaves. Between-clone choice tests compared NE332 constitutive versus NC11382 directly damaged, and NE332 directly damaged versus NC11382 directly damaged, leaves. Leaf disk consumption was measured with a LI-COR 3100 area meter. Larval preference in each petri dish was calculated as a relative feeding index (RF), ranging from 0 to 1.0 (zero indicating no preference), to account for differences in total consumption among petri dishes: $RF = (\text{consumption of preferred leaf disk} - \text{consumption of nonpreferred leaf disk}) \div (\text{consumption of preferred leaf disk})$.

Effect of Prior Herbivory on Larval Movement

Pairs of trees, each containing a constitutive and a previously damaged NC11382 ($n = 6$ pairs), or NE332 ($n = 6$ pairs), were tied together with twist-ties in the glasshouse. On plants with prior forest tent caterpillar damage (defoliation on NC11382 15.2% and on NE332 7.2%), the extent of feeding on each leaf was delimited with black ink fine point permanent marker. Corresponding leaves on constitutive plants were similarly marked. Twenty-five L2 larvae were released in the upper third of each pair of trees and allowed to feed for 4 days. Subsequent defoliation on constitutive trees and new defoliation on previously damaged trees (feeding beyond the ink marks) was measured as described previously. RD was calculated for each pair. Consumption per leaf position was recorded to assess within tree larval feeding preference.

Effect of Prior Herbivory on Larval Development

The effects of previous forest tent caterpillar feeding on subsequent larval development were examined in the glasshouse. Two potential influences on larval activity were considered, herbivory and silk deposition. Eight trees each from NC11382 and NE332 were defoliated 10–27 and 2–19%, respectively, by forest tent caterpillars. Leaf No. 5 on 4 constitutive plants of each clone was coated with silk by herding 10 L3 larvae for 5–10 min. to control for the presence of silk on the defoliated plants. Eight constitutive trees per clone did not receive silk. Ten L2 larvae were group weighed (± 0.1 mg) and placed on leaf No. 5 on each tree. Larval survival and group weight on each tree were recorded after 6–7 days of feeding.

Foliar Analyses of Clones and Larval Responses to Foliar Extracts

Foliar Analyses

Foliar analyses were conducted on constitutive and previously damaged glasshouse clones NC11004, NC11382, NM6, and NE332. Damaged trees had been fed on by forest tent caterpillars for 6–40 days.

Leaf toughness was measured on leaf No. 4 from 5 constitutive and 5 previously damaged trees (directly damaged leaves only). A hand-held penetrometer (McCormick Fruit Tech, Yakima, WA) recorded the force (± 1.0 g) required to puncture 12 interveinal areas per leaf with a 0.647 mm² flat-ended rod (Robison and Raffa 1994). Leaf moisture contents were determined for leaf No. 4 on 4 trees of each clone and condition. Leaves were cut and put in plastic bags in a cooler, and within 1 hr, fresh weights without petioles were recorded (± 0.1 mg). Leaves were then oven-dried at 65°C to constant weight. Leaves from previously damaged trees were a composite of directly and systemically damaged leaves.

Leaf Nos. 3–8 without petioles from 4 trees of each clone and condition were washed in distilled water, oven-dried at 65°C, and ground to a fine powder in a Wiley Mill (Swedesboro, NJ). Leaves from previously damaged trees were a composite of directly and systemically damaged leaves. Leaf total Kjeldahl nitrogen, acid detergent fiber (cellulose + lignin), and neutral detergent fiber (cellulose + lignin + hemicellulose) were determined by the Univ. of Wisc.-Madison, Extension Service, Soil and Plant Analysis Laboratory.

Effects of Foliar Extracts on Second-Instar Feeding Preferences

Polar and nonpolar foliar constituents were extracted from glasshouse constitutive and previously damaged clones NC11382 and NE332, and constitutive clones NC11004 and NM6. Previously damaged trees were 10–20% defoliated by forest tent caterpillars immediately prior to sampling. Leaf Nos. 3–8 were excised in the morning from 6–22 trees of each clone and condition, and stored briefly in plastic bags at 1°C.

A 50.0 g (± 0.3 g) fresh weight sample of leaves without petioles was prepared for each clone and condition. Approximately equal numbers of leaves from positions 3–8 were

included in each sample, but the total number per sample varied due to clonal differences in individual leaf weight. Samples from previously damaged NC11382 and NE332 trees contained 6% and 5% directly damaged leaves, respectively, the remainder being systemically damaged leaves. Leaves were washed in distilled water [to remove dust; silk, frass and exuviae on damaged leaves; and rare mites (Acari: Tetranychidae)] and then ground to ca. 1.0 mm² pieces in liquid nitrogen in a ceramic mortar and pestle. Frozen ground samples were put in 200 ml hexane at 7°C, and extracted in darkness for 8 hours at –28°C. 160 ml of 3:1 MEOH:H₂O at 7°C was added to each flask, and the mixture further extracted in darkness for 8 hr at –28°C. Mixtures were vacuumed through a 0.4–5.5 μ m ceramic filter and the hexane and MEOH:H₂O portions of the solute were separated. Leaf tissue residue was added to 40 ml of ethyl acetate at 7°C and extracted in darkness for 8 hr at –28°C. The ethyl acetate extracts were filtered, added to the MEOH:H₂O extracts. Extracts were brought up to 200 ml with 3:1:1 MEOH:H₂O: Ethyl Acetate, or Hexane, and stored in darkness at –28°C. Ten ml aliquots of each polar and nonpolar extract were oven-dried (65°C) to constant weight (± 0.1 mg). Leaf dry weight (65°C) determinations (± 0.1 mg) were made from a second composite sample of leaf Nos. 3–8 from each clone and condition ($n = 4$).

Larval responses to leaf extracts were examined by coating 1.1 cm² excised leaf disks with the above extracts. Leaf disks from constitutive NC11004 (leaf No. 4) served as the substrate for the extract coatings due to its high suitability for the forest tent caterpillar (see Table 2, Robison and Raffa 1994). Leaf disks were coated with 0.06 ml (3 drops from a 1 ml pipette) of the extracts, which corresponds to the approximately 0.052 ml of these extracts present in equivalent foliage (2.5 mg dry weight/leaf disk). Treated leaf disks were used in 2-choice assays with 3 L2 larvae in 5 cm petri dishes for 24 hr, as described previously ($n = 10$ –13 for each choice test). Assays of polar and nonpolar extract treatments were NC11382 constitutive versus NC11382 damaged, NE332 constitutive versus NE332 damaged, and NC11382 constitutive versus NE332 constitutive. RF was calculated as described previously.

Population Responses to Clones

A field study was conducted to determine if clonal effects on larval performance in laboratory and glasshouse studies could affect population dynamics. Wood-framed cages were constructed around clones NC11382 and NE332 at the start of their 2nd growing season. Each cage enclosed two 2.0–2.5 m tall trees of the same clone ($n = 6$ cages per clone). Cage frames, 1.22 \times 2.44 \times 1.22 m tall, were anchored to the ground and covered with white nylon insect screens (described previously). Screens were 1.22 \times 2.44 \times 4.88 m tall, with an open bottom. The bottom 30–60 cm of each screen was buried around the frame base, and the remainder hung loosely about the frame to allow the enclosed trees to grow and expand the cage. One edge of each cage was sealed with clips to allow interior access. Temperature and RH in the cages were within 2°C and 2%, respectively, of those recorded outside the cages near midday.

Two forest tent caterpillar egg bands containing similar numbers of total eggs (Witter and Kulman 1969) were suspended on one tree per cage in mid-June of Year 1 (1989). Egg bands were hung approximately 30 cm apart and within 18 cm of branch tips. Trees within cages were linked with 2 loose circles of string to facilitate caterpillar movement between the trees. Populations were allowed to develop for 2 yr.

Larvae were collected, group weighed (± 0.1 g), and returned to each cage twice in Year 1, and 3 times in Year 2. Sample size varied from 3–229, depending on the population in each cage. An additional larval sample (L3/L4) in Year 2 [Day of Year (DoY) 155] (larvae from NC11382 = 14 ± 3 /cage; from NE332 = 7 ± 2 /cage) was collected but not returned to the cages. These larvae were laboratory-reared on foliage and artificial diet to measure parasitization. Those insects which pupated in the laboratory were counted in the pupal survey results for Year 2 ($n = 3$ pupae/cage for both NC11382 and NE332; see Table 11). Defoliation was visually estimated ($\pm 5\%$) in each cage in Year 2 during the pupal stage. All pupal cases were collected from the cages, leaf litter, and trees each year after oviposition. Pupal cases were sexed (Muggli 1974), and the width of the first abdominal segment visible posterior to the wing pads was measured (± 0.1 mm), in Year 1.

Egg bands were counted during the pupal collections each year, and those which were tight on twigs were marked with colored flagging and loosely covered with paper tape to further secure them for overwintering from Year 1 to 2. Loose egg bands on twigs, and those on petioles and weeds were collected, stored overwinter in an insulated outdoor box between Year 1 and 2, and then reattached to the trees in their respective cages and marked with colored flagging prior to budbreak in Year 2. After oviposition in Year 2, flagged egg bands from Year 1, and unflagged and unhatched egg bands from Year 2, were collected. The numbers of hatched and unhatched eggs in each egg band from Year 1 were counted directly. Egg bands from Year 2 were stored overwinter in an insulated outdoor box, hatched in the laboratory the following spring, and then counted.

Stage specific female populations in Years 1 and 2 were averaged, and life tables were calculated for each clone. The numbers of eggs, L1 larvae (= number of viable eggs), and pupae in both years were adjusted to females by using the % female pupae data from Year 1. This was done because only adult females could be estimated from the number of egg bands. The mortality factors identified were egg nonviability (counted directly), larval mortality (number of hatched eggs – number of pupae), and pupal-adult nonviability (number of pupae – number of egg bands).

Statistical Analysis

The general linear models procedure of analysis of variance (GLM ANOVA) was used, and when significant differences were found means were separated by the Tukey (HSD) Compromise, or Fisher's LSD techniques (Abacus Concepts 1989). Variance homogeneity was evaluated graphically for each analysis, and data were transformed as needed. Initial insect weight in developmental tests, and total consumption

per petri dish in behavioral tests, were not significant covariates in these analyses. RD and RF indices were tested for significance (\neq zero) by $t = \bar{x}_i / \sqrt{(MSE/n_i)}$, with MSE derived from a GLM ANOVA among the preference tests. Pearson product-moment correlations and simple linear regressions were calculated. Categorical data were analyzed by Chi-square, and Kruskal-Wallis global nonparametric test (K-W Test) for independence among groups (H statistic corrected for ties among groups) (Abacus Concepts 1987). Differences between slopes were evaluated by

$$t_{n-2} = (|\text{slope}_1 - \text{slope}_2|) / \sqrt{([SE_1]^2 + [SE_2]^2)}$$

Results

Larval Responses to Constitutive Variation Among Clones

Effect of Bud Surface Characteristics on

First-Instar Mobility

Copious amounts of yellow resinous plant exudates were observed on the opening buds and newly expanding foliage of clone NC11382, but not on NE332, in the field and glasshouse. Leaves which had matured into position No. 1 on NC11382 were considerably drier than younger leaves. No L1 larvae were able to feed or move off NC11382 buds after 30 min. or 24 hr on glasshouse trees (Table 1). On NE332 buds in the glasshouse approximately one-third and one-half of the larvae could move after 30 min. and 24 hr, respectively (Table 1). Similar relative results were obtained in the field, but the ability of bud exudates to impair larval mobility was somewhat reduced (Table 1).

Methanol extracts of NC11382 and NE332 bud surfaces yielded substantially different HPLC profiles (Robison 1993). The cumulative height of NC11382 peaks was 3.8 \times greater than the NE332 peaks. The amount of dry weight extractable material on a mg/cm bud length basis was greater on NC11382 than NE332 buds, 0.64 mg/cm and 0.41 mg/cm, respectively. However, the amount of extractable material on a mg/mg bud dry weight basis was nearly equivalent on NC11382 and NE332 buds, 0.08 mg/mg and 0.10 mg/mg, respectively.

Effects of Clonal Suitability on Early-Instar Movement

First-instar larvae dispersed more slowly and in smaller numbers from NC11004 than from NC11382, NM6, and NE332 (Table 2). Linear regressions between days and cumulative percent L1 dispersal were significant for all 4 clones, but the intercepts were not (Table 2) (regressions

Table 1. Percentage of L1 forest tent caterpillars on buds of hybrid poplar clones immobilized by exudates, by type of environment and time since placement.

Clone	Glasshouse trees			Field trees	
	After 30 minutes	After 24 hours	<i>n</i>	After 30 minutes	<i>n</i>
NC11382	100	100	14	62	8
NE332	64	45	11	12	8
Chi-square =	6.06	10.05		4.27	
	(<i>P</i> = 0.0138)	(<i>P</i> = 0.0015)		(<i>P</i> = 0.0389)	

Table 2. Dispersal ($\bar{x} \pm s$) of L1 forest tent caterpillars after hatching on hybrid poplar clones; all data square root transformed for statistical analysis.

Clone	% dispersal ¹ day 5	% dispersed within ² 0.6 cm of stem	Linear regression of % dispersing by day ³					
			Slope (B ₁)	Intercept (B ₀)	r ²	df	F	P
NC11004	4.7 ± 0.7b	1.0 ± 1.1	0.45b	-0.16	0.44	1,22	16.97	0.0004
NC11382	21.8 ± 14.9ab	9.1 ± 11.2	0.99a	-0.21	0.68	1,17	35.85	0.0001
NM6	28.4 ± 13.5a	4.9 ± 4.6	1.10a	-0.71	0.78	1,25	88.65	0.0001
NE332	41.1 ± 21.4a	10.6 ± 6.1**	1.10a	0.02	0.72	1,34	88.23	0.0001

¹ $F_{3,13} = 6.66$, $P = 0.0058$, means followed by different letters significantly different at $P = 0.05$ (Tukey compromise separations).

² $F_{3,14} = 2.83$, $P = 0.0764$, ** indicates significantly different than 0.0 at $P = 0.05$.

³ Slopes followed by different letters are significantly different at $P = 0.10(t_{n-2} = (slope_x - slope_{xi}) / (\sqrt{[SE_x]^2 + [SE_{xi}]^2}))$.

calculated on the basis of 1st-instar duration: 5 days on NC11004 and NC11382, 8 days on NM6 and NE332. Most (89–99%) larvae dispersed by dropping from branches and leaves and landing distal to the tree stems. Only 1.0–10.6% of the dispersed larvae were found close to the tree stems (Table 2). Dispersal among clones on day 5 was negatively correlated with larval survival ($r = -0.94$, $P \leq 0.05$) and larval weight ($r = -0.98$, $P \leq 0.01$), and negatively, but weakly correlated with L2 feeding preferences ($r = -0.71$, $P > 0.10$) (from Table 2 and Robison 1993).

In mixed-tree blocks larval colonies (L1–L2) spent 7.4 days on clone NC11004 and only 3.8 days on NM6 (Table 3). In uniform blocks, colonies generally fed within the clonal blocks in which they hatched, spending statistically equivalent time on clones NC11004 and NM6, 4.6 and 6.6 days, respectively (Table 3). In choice tests with clones tied together, larvae defoliated clone NC11004 significantly more than NM6, and clone NC11382 significantly more than NE332 (Table 4).

Effect of Leaf Position on Early-Instar Feeding Preference

The suitability of leaf positions (= age) for larval feeding varied within and between constitutive clones. Leaf disks from position Nos. 4 and 6, and 2, 4, and 6, were preferred from clones NE332 and NC11382, respectively (Figure 2). Total consumption was greater on NC11382 than NE332 leaf disks. Leaf disks from NE332 leaves 1, 2, 12, and 14 were avoided, while on NC11382, disks from leaves 10, 12, and 14 were avoided (Figure 2). The location and amount of larval feeding on whole-plants (from the experiments summarized in Tables 4 and 7) indicate that larvae on constitutive plants

generally prefer leaf Nos. 2–7 on NC11004 and NM6, and positions 3–7 on NC11382 and NE332 (Figure 3).

Effects of Clonal Switching on Larval Development

In the sequential host developmental assay, larvae were significantly heavier on NC11382 than on NE332, 3.04, and 1.14 mg, respectively, after 5 days of feeding (Figure 4). Relative differences between these clones in larval growth increased from 2.7× after 5 days of feeding to 4.8× after 10 days. The effect of switching between clones on larval growth depended on sequence. Larvae which initially consumed NC11382 and then were switched to NE332 grew equivalent to larvae which spent all 10 days on NE332 (Figure 4). Larvae which initially consumed NE332 and then were switched to NC11382 grew equivalent to those which spent all 10 days on NC11382. Larval survival did not differ between NC11382 and NE332 after 5 days of feeding (91 and 88%, respectively: $F_{1,22} = 0.22$, $P = 0.6441$). Survival after 10 days differed only slightly among the clonal diets, 87% on NC11382, 84% on NE332, 91% on NC11382 then NE332, and 76% on NE332 then NC11382 ($F_{3,19} = 2.35$, $P = 0.1047$).

Effects of Silk and Group Size on Larval Behavior and Development

Larval silk significantly enhanced the steadfastness of L1 and L2 forest tent caterpillars (Figure 5). Larvae were 3× more likely to maintain their steadfastness on leaves coated with silk.

Early-instar larval survival, development, and consumption were significantly enhanced by increasing group size (Table 5). Preexisting larval silk on leaves generally enhanced larval success in cohorts of 1 and 2 individuals. In larger groups, the effects of silk were smaller. Differences in larval development and consumption between groups ranging from 1–10 individuals were greater on unsilked leaves than on leaves treated with silk. Increasing cohort size from 2 to 3, from 2 to 5, and from 5 to 10, approximately doubled, quadrupled, and tripled consumption, respectively, on both silked and control leaves. Single larvae on unsilked leaves remained as L1 throughout the assay, but all single larvae on silked leaves reached the 2nd-instar. In cohorts of 10 on silked leaves, 4% of the larvae reached the 3rd instar and none remained as L1. In all other groups larvae were 11–40% L1 and 60–89% L2 at the end of the assay.

Table 3. Forest tent caterpillar colony movement (L1–L2) among hybrid poplar clones planted in two arrangements (see Figure 1).

Clonal arrangement	Number of days on each clone ± s		df	Chi-square	P
	NC11004	NM6			
Uniform blocks	4.6 ± 1.9	6.6 ± 1.8	4	5.161	0.2712
Mixed-tree blocks	7.4 ± 2.5	3.8 ± 2.9	4	12.033	0.0171

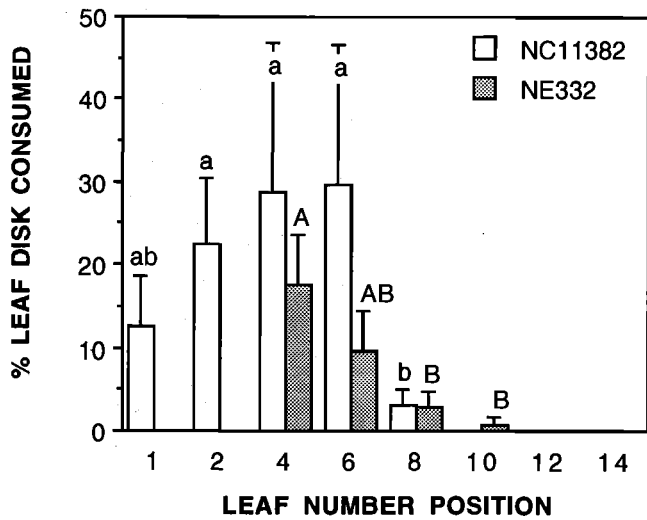


Figure 2. Consumption (+s_e) of leaf disks excised from sequential leaf positions from constitutive clones NC11382 and NE332, in petri dish choice tests. Different letters, by clone, indicate statistical significance at the $P = 0.05$ level, by Fisher's protected LSD separations technique: NC11382, $F_{7,32} = 3.60$, $P = 0.0058$; NE332, $F_{7,31} = 8.19$, $P = 0.0001$.

Table 4. Early-instar forest tent caterpillar feeding preferences among constitutive, potted hybrid poplar clones, tied together; relative defoliation defined in text; *, ** indicate significance from 0.0 at $P = 0.10$ and 0.05 , respectively ($t_{n-1} = \bar{x}_j / \sqrt{(MSE/n_j)}$, where $MSE = 0.4241$ from ANOVA $F = 0.33_{1,13}$, $P = 0.5741$).

Clone	Preferred choice		Nonpreferred choice		Relative defoliation ± s
	% defoliation	Clone	% defoliation	n	
NC11004	12.7	NM6	5.2	8	0.44 ± 0.72*
NC11382	8.9	NE332	2.2	7	0.64 ± 0.57**

Larval Responses to Previously Damaged Clones

Effect of Prior Injury on Second-Instar Feeding Preference

In 2-choice petri dish assays, larvae significantly preferred leaf disks from constitutive plants over those from systemically—or directly—damaged leaves of clones NC11382, NE332, and NC11445 (Table 6). The intensity

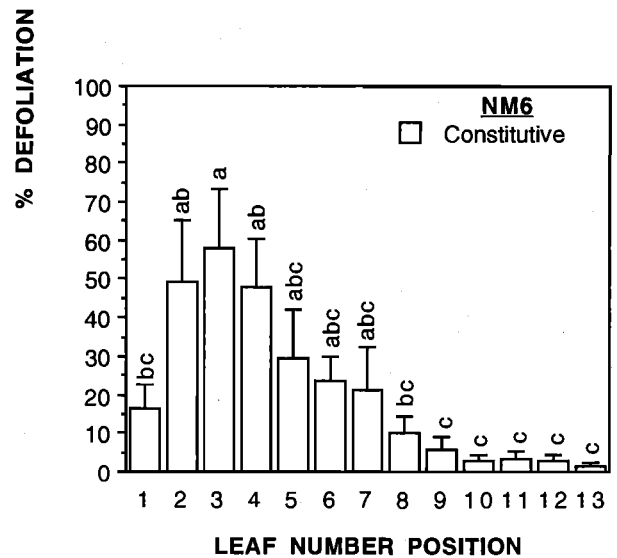
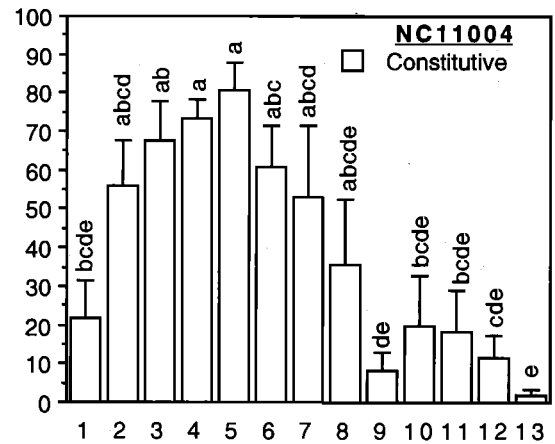
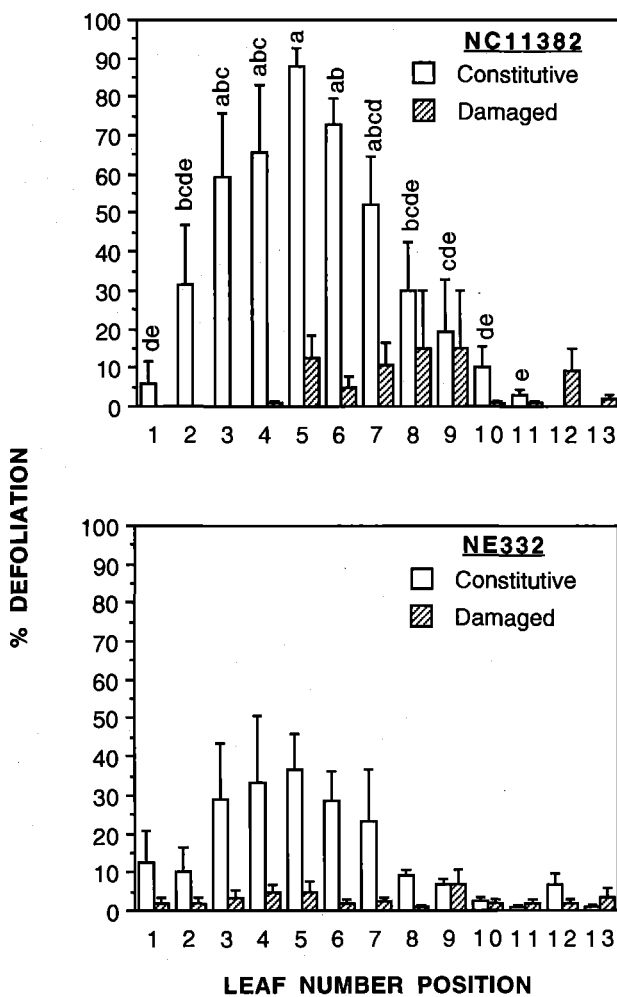


Figure 3. Percent defoliation (+s_e) on leaf positions 1-13 by L1-L3 forest tent caterpillars on constitutive and previously fed upon (damaged) hybrid poplar clones, in a glasshouse. Different letters indicate statistical significance at the $P = 0.05$ level, by the Tukey compromise separations technique; for NC11382-constitutive $F_{12,78} = 8.39$, $P = 0.0001$; for NC11382-damaged $F_{12,65} = 0.85$, $P = 0.5955$; for NE332-constitutive $F_{12,65} = 2.26$, $P = 0.0185$; for NE332-damaged $F_{12,65} = 0.89$, $P = 0.5583$; for NC11004-constitutive $F_{12,65} = 6.62$, $P = 0.0001$; and for NM6-constitutive $F_{12,78} = 4.91$, $P = 0.0001$.

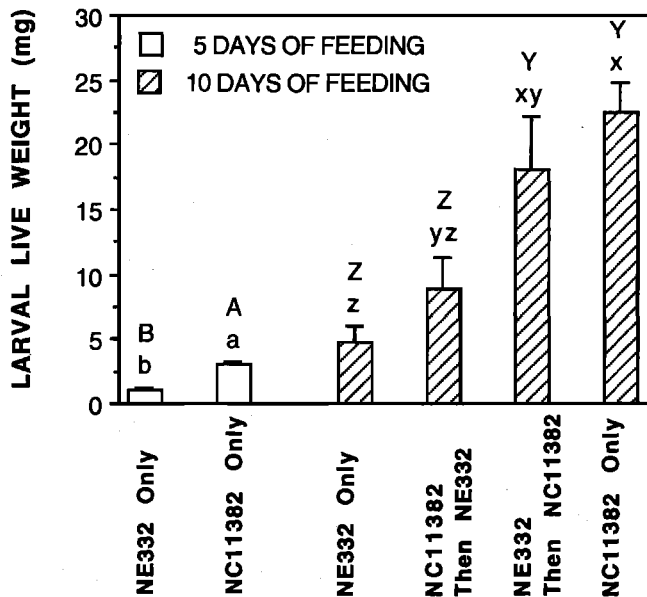


Figure 4. Effect of sequence of feeding on 2 hybrid poplar clones on forest tent caterpillar weight ($\pm s_x$). After 5 days of feeding on NC11382 or NE332, $F_{1,22} = 49.26$, $P = 0.0001$. After 5 additional days on the same clone or on the "opposite" clone, $F_{3,19} = 7.95$, $P = 0.0012$. Different letters indicate statistically different means at $P = 0.05$, lower case letters from the Tukey compromise separations technique; upper case letters from Fisher's protected LSD separations technique.

of induction, as measured by RF, was equivalent between systemically and directly damaged leaves from each clone. Among clones, systemically damaged leaves were also equivalently induced. However, the intensity of induction in directly damaged leaves was significantly greater in clone NC11445 than in NC11382, while NE332 was intermediate. Leaf disks from constitutive NE332 were preferred over those from directly damaged NC11382. Leaf

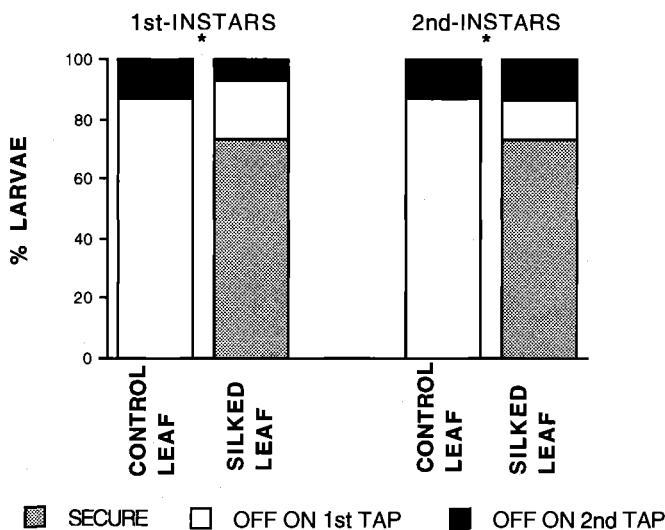


Figure 5. Effect of larval silk on steadfastness of 1st- and 2nd-instar forest tent caterpillars. Larvae were dropped individually onto the top surface of a leaf and allowed 3–5 seconds before the bottom of the leaf was tapped. Leaves were either untreated control or top surface experimentally coated with forest tent caterpillar silk. * indicates a significant leaf treatment effect: 1st-instars Chi Square₁₅ = 17.58, $P = 0.0002$; 2nd-instars Chi Square₁₅ = 19.07, $P = 0.0001$.

Table 5. Effects of L1 forest tent caterpillar cohort size and conspecific silk on leaves on larval development and consumption ($\pm s$) for 6 days on hybrid poplar clone NC11004 in the laboratory; means in column followed by different letters significantly different at $P = 0.05$ (Tukey compromise separations).¹

Larvae per cohort	Leaf treatment	n	% survival	Final weight (mg)/larvae	Leaf consumption (cm ²)/cohort
1	Control	8	12 \pm 35b	0.3 \pm 0c	0.1 \pm 0.1d
	Silked	9	44 \pm 53ab	3.2 \pm 2.4ab	1.3 \pm 1.0bc
2	Control	6	42 \pm 38ab	1.4 \pm 1.2bc	1.2 \pm 1.0c
	Silked	6	75 \pm 42ab	2.6 \pm 1.5ab	1.4 \pm 0.8bc
3	Control	5	100 \pm 0a	3.6 \pm 2.2ab	2.9 \pm 2.8bc
	Silked	5	53 \pm 45ab	3.2 \pm 2.0ab	2.8 \pm 2.0abc
5	Control	5	96 \pm 9a	4.0 \pm 2.2ab	5.5 \pm 2.8abc
	Silked	5	76 \pm 33ab	3.5 \pm 2.0ab	6.0 \pm 4.1abc
10	Control	5	98 \pm 4a	5.3 \pm 3.0ab	13.1 \pm 6.1ab
	Silked	5	98 \pm 5a	7.4 \pm 0.8a	17.9 \pm 3.7a

¹ Survival $F_{9,49} = 4.82$, $P = 0.0001$; final weight log transformed for statistical analysis, $F_{9,33} = 3.87$, $P = 0.0020$; leaf consumption log transformed for statistical analysis, $F_{9,31} = 8.39$, $P = 0.0001$.

disks from directly damaged NC11382 were preferred over those from directly damaged NE332. Correlations for each clone between percent defoliation of each damaged plant and the RF resulting from each choice test were positive, but not significant.

Effect of Herbivory on Larval Movement

Larvae preferred constitutive over previously damaged whole plants of NC11382 in 2-choice tests (Table 7). Constitutive plants were also preferred over previously damaged plants of NE332, but not significantly. Although larvae generally preferred leaf Nos. 3–7 on constitutive NC11382 and NE332 (Figure 3; from Table 7), on previously damaged plants they tended to feed more evenly among a greater number of leaf positions, and consumed significantly less foliage (Figure 3).

Effect of Prior Herbivory on Larval Development

Prior herbivory on whole plants significantly reduced larval weight gain on clones NC11382 and NE332 by 66 and 68%, respectively (Table 8). Experimental silking on leaf No. 5 (the point of larval release) on constitutive plants only slightly improved larval weight gain on NC11382 and NE332, by 5 and 1%, respectively. Survival was not affected by previous damage or silking, although survival on NE332 was substantially lower on damaged than on constitutive trees (49 versus 74–85%). Correlations between the amount of defoliation on each tree and insect weight gain were negative, but not significant.

Foliar Analyses of Clones and Larval Responses to Foliar Extracts

Foliar Analyses

Leaf nitrogen was significantly lower in constitutive NM6 (3.36%) than in constitutive NC11004, NC11382, and NE332 (4.5–4.7%) (Table 9). Foliar nitrogen was significantly lower in damaged than in constitutive leaves from clones NC11382 (3.8 versus 4.7%) and NE332 (3.3 versus 4.6%). Moisture content did not vary greatly among clones or between constitutive and damaged trees, except in NE332 where it was

Table 6. Feeding preference (\pm s) of L2 forest tent caterpillars between leaf disks from constitutive, and previously directly and previously systemically damaged leaves of hybrid poplar clones in 2-choice petri dish assays; relative feeding defined in text; * indicates a significant preference at $P=0.01$ (by $t_{n-1} = \bar{x}_i/\sqrt{(MSE/n_i)}$, where $MSE = 0.1813$ from ANOVA $F = 12.01_{8,167}$, $P = 0.0001$); within clone choice tests ANOVA $F_{5,143} = 3.21$, $P = 0.009$, means followed by different letters significantly different at $P = 0.05$ (Tukey compromise separations).

Clone	Preferred choice		Nonpreferred choice			n	Relative feeding
	Condition	% consumed	Clone	Condition	% consumed		
Within clone choice tests							
NC11382	Constitutive	59.7 \pm 29.2	NC11382	Systemic	17.6 \pm 13.6	28	0.61 \pm 0.41ab*
NC11382	Constitutive	49.1 \pm 30.0	NC11382	Directly	25.6 \pm 24.2	24	0.32 \pm 0.65b*
NE332	Constitutive	35.7 \pm 27.1	NE332	Systemic	6.4 \pm 6.7	24	0.70 \pm 0.45a*
NE332	Constitutive	31.9 \pm 24.7	NE332	Directly	7.6 \pm 5.2	22	0.55 \pm 0.50ab*
NC11445	Constitutive	66.0 \pm 20.9	NC11445	Systemic	14.1 \pm 9.4	28	0.73 \pm 0.23a*
NC11445	Constitutive	24.6 \pm 20.3	NC11445	Directly	4.4 \pm 3.3	23	0.74 \pm 0.31a*
Between clone choice tests							
NC11382	Directly	83.2 \pm 22.5	NE332	Constitutive	27.0 \pm 13.6	9	0.63 \pm 0.28*
NC11382	Directly	70.4 \pm 33.6	NE332	Directly	12.0 \pm 9.4	9	0.82 \pm 0.15*

significantly lower in damaged than in constitutive leaves (77 versus 83%). Leaf acid detergent fiber (ADF) did not vary among constitutive clones, but was higher in damaged than constitutive NC11382 and NE332. Leaf neutral detergent fiber (NDF) among constitutive trees was highest in NC11382, lowest in NM6, and intermediate in NC11004 and NE332. Reliable NDF data from damaged plants were only available from NE332, where it was significantly higher than in constitutive NE332. Leaf toughness did not vary among constitutive clones, but was significantly higher in damaged than in constitutive NC11382, NE332, and NM6.

The only significant correlation between constitutive foliar characteristics and larval behavior or development was between L2 preference (Robison 1993) and NDF ($r = 0.91$, $P \leq 0.05$) (from Tables 2, 9).

Effects of Foliar Extracts on Second-Instar Feeding Preferences

Larvae significantly preferred leaf disks treated with polar extracts from constitutive leaves, over those from damaged leaves for clones NC11382 and NE332 (Table 10). Similarly, nonpolar extracts from constitutive NC11382 and NE332 leaves were preferred over nonpolar extracts from damaged leaves, for both clones. Larvae preferred leaf disks treated with the polar constitutive extract of NC11382 over the polar constitutive extract of NE332. However, larvae weakly preferred leaf disks treated with the nonpolar NE332 constitutive extract over those treated with the nonpolar NC11382 constitutive extract.

Population Responses to Clones

Forest tent caterpillar populations were differentially affected by clones NC11382 and NE332 in field cages (Table 11). The mean number of eggs per cage increased by 7.0 \times during Year 1, and by 1.4 \times during Year 2 (9.7 \times overall) on clone NC11382. On NE332, however, the mean number of eggs per cage increased by only 1.1 \times during Year 1, and declined by 2.9 \times during Year 2 (-2.7 \times overall). Fecundity and egg viability did not differ between clones in either year. In both years a small number of parasitized eggs were counted as unhatched. The number of pupae per cage increased between Years 1 and 2 on NC11382 and NE332 by 2.5 \times and 1.4 \times , respectively. Female and male pupal widths were equivalent between clones in Year 1. The percent female pupae was also equivalent on both clones in Year 1. Foliage was not limiting in Year 1 or 2 on either clone. Mean defoliation in Year 2 on NC11382 and NE332 was 23% and 6%, respectively ($F_{1,9} = 6.11$, $P = 0.0355$).

Larvae grew larger on NC11382 than on NE332 in Year 1, when artificially applied egg bands had peak hatch 44 days after spring budbreak on both clones (Figure 6). However, larvae were significantly heavier on NE332 than on NC11382 in Year 2, when budbreak and egg hatch were in natural synchrony, occurring within 1 day of each other on both clones. Larval growth rates on both clones were faster in Year 1 than Year 2 (Figure 6).

The highest mortality in both years occurred during the larval stages on both clones (Table 12). On clone NC11382,

Table 7. Early-instar forest tent caterpillar feeding preferences between constitutive and forest tent caterpillar damaged, potted hybrid poplar clones, tied together; previous defoliation on NC11382 = 15.2%, on NE332 = 7.2%; relative defoliation defined in text; * indicates significance from 0.0 at $P=0.01$, respectively (by $t_{n-1} = \bar{x}_i/\sqrt{(MSE/n_i)}$ where $MSE = 0.1727$ from ANOVA $F = 3.80_{1,10}$, $P = 0.0796$).**

Clone	Preferred choice		Nonpreferred choice			n	Relative defoliation \pm s
	Condition	% defoliation	Clone	Condition	% defoliation		
NC11382	Constitutive	25.2	NC11382	Damaged	6.0	6	0.77 \pm 0.18***
NE332	Constitutive	1.8	NE332	Damaged	0.9	6	0.30 \pm 0.56

Table 8. Effects of forest tent caterpillar herbivory and silk on potted poplar clones on the quality of the foliage for subsequent forest tent caterpillar larval development; means followed by different letters significantly different at $P = 0.05$ (Tukey compromise separations).

Clone	Condition	% survival $\pm s^1$	Growth $\pm s^2$ (mg/day)
NC11382	Constitutive	90 \pm 8	4.77 \pm 2.54a
	Constitutive-silked	84 \pm 18	5.02 \pm 2.11a
	Damaged (prior defoliation = 17%)	85 \pm 15	1.60 \pm 0.62b
NE332	Constitutive	85 \pm 19	4.10 \pm 1.84y
	Constitutive-silked	74 \pm 24	4.16 \pm 2.39y
	Damaged (prior defoliation = 7%)	49 \pm 34	1.33 \pm 0.90z

¹ NC11382: $F_{2,17} = 0.22$, $P = 0.8062$; NE332: $F_{2,17} = 2.74$, $P = 0.0933$.

² Data log transformed for statistical analysis for both clones; NC11382: $F_{2,17} = 16.95$, $P = 0.0001$; NE332: $F_{2,17} = 10.35$, $P = 0.0011$.

16% and 31% more larvae died than eggs or pupae-adults, respectively (Table 12). On clone NE332, 39% and 4% more larvae died than eggs or pupae-adults, respectively. Parasitism of L3/L4 larvae on NC11382 and NE332 was 7 and 8%, respectively, in Year 2.

Discussion

Constitutive and induced foliar characteristics of hybrid poplar clones differentially affected forest tent caterpillar behavior, development, and population growth. Previously reported experiments with constitutive plants and forest tent caterpillars found that NC11004 and NC11382 were high quality hosts, NC11445 was an intermediate quality host, and NM6 and NE332 were poor quality hosts for this insect ($P \leq 0.05$, in Robison and Raffa 1994, Robison 1993). Significant correlations among larval behavioral and developmental parameters for these 4 clones indicated that the suitability of each clone can be characterized in several ways [Robison and Raffa 1994, from Robison (1993): survival and weight ($r = 0.96$, $P \leq 0.05$), survival and L2 preference [$r = 0.88$, $P \leq 0.05$], weight and L2 preference [$r = 0.71$, $P > 0.1$]].

First-instar forest tent caterpillars dispersed more rapidly and in greater numbers from less suitable clones (Table 2). This behavior has not previously been reported for this insect. Most larvae dispersed by dropping from trees by silken threads in a solitary, nondirected fashion, which fractures colonial aggregations. Only a small proportion of the dis-

persed insects (1–11 %) aggregated near the base of the trees. Nondirected dispersal differs from the within-colony communication and movement (colonial nomadic foraging) typical on suitable hosts (Fitzgerald and Costa 1986). Dispersal on silk threads due to poor host quality or dense populations may contribute to population movements, and possibly spread outbreaks as described for other Lepidopteran forest defoliators (Berryman and Safranyik 1980). In dense populations, new aggregations may form when individual larvae land in close proximity on new hosts.

The probability of a randomly dispersing larva reaching a suitable host varies with location, weather, and plant species composition. The benefits of colonial structure, such as enhanced larval development and steadfastness (Table 5; Figure 5), defense, thermoregulation, and food finding (Fitzgerald and Peterson 1988, Knapp and Casey 1986, Peterson et al. 1987), are sacrificed by nondirected dispersal. However, these risks may be offset by the developmental and population benefits of replacing a poor quality with a high quality host (Table 12, Figure 4, Stoyenoff et al. 1994a, 1994b).

The deposition of silk and trail pheromones with each step guides larvae to food or resting sites, maintains colony cohesion (Berenbaum et al. 1993, Fitzgerald and Costa 1986) and facilitates re-aggregation of dispersed caterpillars. Larvae released on previously damaged poplars immediately follow old silk trails and disperse throughout the plant. However, the larval cohort soon re-coalesces on the leaf upon

Table 9. Foliar characteristics ($\pm s$) of glasshouse grown constitutive and forest tent caterpillar damaged hybrid poplar clones; means in a column followed by different letters are significantly different at $P = 0.05$ (Tukey compromise separation); data not followed by a letter $n = 1$, otherwise $n = 4$; for each clone and column *, **, and * indicates significance between constitutive and damaged condition at $P = 0.1$, 0.05, and 0.01, respectively (paired t-test analysis of variance).**

Clone	Condition	Nitrogen ²	Moisture ³	ADF fiber ⁴	NDF fiber ⁵	Toughness ⁶
NC11004	Constitutive	4.50 \pm 0.18a	84.4 \pm 1.4a	25.3 \pm 1.8b	29.2 \pm 1.6bc	13.6 \pm 5.9ab
	Damaged	4.62	83.4 \pm 1.2a	23.7	—	14.6 \pm 4.8ab
NC11382	Constitutive	4.68 \pm 0.17a***	83.2 \pm 0.7a	27.4 \pm 2.9b	33.6 \pm 4.0ab	12.7 \pm 3.4ab**
	Damaged	3.81 \pm 0.34b	81.0 \pm 2.5a	30.9 \pm 4.1a	35.6	22.6 \pm 6.2a
NE332	Constitutive	4.61 \pm 0.20a***	83.3 \pm 0.6a***	22.9 \pm 1.9b**	27.7 \pm 2.0bc*	11.2 \pm 5.2b*
	Damaged	3.28 \pm 0.13b	76.9 \pm 1.1b	27.7 \pm 0.6b	31.1 \pm 1.6abc	19.1 \pm 6.2ab
NM6	Constitutive	3.36 \pm 0.06b	81.5 \pm 0.6a	25.3 \pm 3.0b	26.9 \pm 1.5c	14.8 \pm 5.4ab*
	Damaged	3.67	82.0 \pm 2.3a	22.0	—	23.0 \pm 5.9a
ANOVA		$F_{7,18} = 30.86$ $P = 0.0001$	$F_{7,24} = 9.96$ $P = 0.0001$	$F_{7,18} = 3.63$ $P = 0.0129$	$F_{5,11} = 5.44$ $P = 0.0092$	$F_{7,32} = 3.46$ $P = 0.0072$

Table 10. Effect of foliar extracts from hybrid poplar clones NC11382 and NE332 on the feeding preference of L2 forest tent caterpillars in 2-choice petri dish assays with extracts from constitutive and damaged leaves applied to leaf disks of constitutive clone NC11004; relative feeding defined in text; *, **, and * indicate significance at $P = 0.01, 0.05,$ and $0.10,$ respectively [$t_{n-1} = \bar{x}_i / \sqrt{(MSE/n_i)}$], where polar extracts $MSE = 0.3238$ (ANOVA $F_{2,33} = 1.51, P = 0.2356$), and nonpolar extracts $MSE = 0.4029$ (ANOVA $F_{2,31} = 6.59, P = 0.0041$).**

Preferred choice		Nonpreferred choice		<i>n</i>	Relative feeding $\pm s$
Clone	Condition	Clone	Condition		
Polar extracts					
NC11382	Constitutive	NC11382	Damaged	11	0.77 \pm 0.19***
NE332	Constitutive	NE332	Damaged	13	0.53 \pm 0.73***
NC11382	Constitutive	NE332	Constitutive	12	0.36 \pm 0.59**
Nonpolar extracts					
NC11382	Constitutive	NC11382	Damaged	12	0.42 \pm 0.70***
NE332	Constitutive	NE332	Damaged	12	0.63 \pm 0.57***
NE332	Constitutive	NC11382	Constitutive	10	0.32 \pm 0.63*

which it was released. This suggests that old and new trails are distinct, that individual larvae may recognize their own trails, and that group feeding at the site of release is more important than trail following to distant food. Similarly, larvae released on leaves that were experimentally silked, but not linked to the rest of the plant with silk trails, explored the leaf on which they were released and then rapidly aggregated to feed. Without a prior silk coating, larvae wandered more tentatively and only slowly formed feeding aggregations. Silk trails also improve larval steadfastness (Figure 5). Thus silk may facilitate feeding arrestment, and the ability of larvae to utilize native trembling/quaking aspens, so-named because of their fluttering leaves.

The critical size for an effective feeding aggregation of early-instar forest tent caterpillars has not previously been evaluated. While colonies typically arise from egg bands containing 80–480 eggs (Witter and Kulman 1969), cohorts may be smaller due to small egg clusters, low egg viability, or groups of larvae coalescing after nondirected dispersal. Two L1 larvae per cohort were required to assure survival, growth, and consumption. Consumption substantially increased between group sizes of 5 and 10 larvae (Table 5). In addition, larvae only reached the 3rd-instar during the 6 day

assay when there were 10/group on previously silked leaves. Because Hodson (1941) determined that approximately 6 days were needed for groups of 15 larvae to reach L3 at similar temperatures, there appears to be little improvement in developmental rate above 10 larvae/cohort. The presence of silk tended to enhance development (Table 5). Therefore, the formation of small aggregations after nondirected early-instar dispersal, facilitated by silk trails, may be sufficient for forest tent caterpillar success.

The presence of conspecific silk may also be an indicator of food suitability (Peterson 1987). However, dense silken mats from high populations deter feeding and perhaps elicit a search for new food. Thus, an equilibrium between the attractiveness of a demonstrated food (i.e., the presence of silk) and declining food quality due to herbivory (Tables 6–8) and silk density may affect the movement of foraging colonies. The fragmentation of colonies during the 3rd instar may be related to factors of scale and host plant resources. Consumption and larval size increase greatly during the 3rd instar (Hodson 1941). Thus, large groups of larvae could not exist on a single leaf or in a restricted area, and induction due to herbivory can cause larvae to disperse (Table 7) and thereby contribute to colony fragmentation.

Table 11. Forest tent caterpillar population characteristics ($\pm s$) in consecutive years on field-caged hybrid poplar clones; spring of Year 1 cages ($n = 6/\text{clone}$) infested with 2 egg bands containing similar numbers of eggs; number of L1 larvae eclosed equivalent between clones (NC11382 = 226 and NE332 = 238 L1/cage; $F_{1,10} = 0.13, P = 0.73$).¹

Characteristic	Year	NC11382	NE332	<i>F</i>	<i>P</i>
Eggs/cage	Spring of 1	344 \pm 9	340 \pm 8	0.83	0.38
	End of 1	2,406 \pm 2,078	358 \pm 202	10.04 Δ	0.01
	End of 2	3,341 \pm 4,026	125 \pm 279	7.48	0.02
Fecundity	1	180 \pm 40	162 \pm 28	0.72	0.42
	2	172 \pm 18	156 \pm 0	0.60 \diamond	0.48
% egg viability	1	54 \pm 13	53 \pm 19	0.00	0.96
	2	30 \pm 22	40 \pm 0	0.27 \diamond	0.63
Pupae/cage	1	52 \pm 36	16 \pm 15	7.01 \diamond	0.02
	2	130 \pm 91	23 \pm 23	7.67 \diamond	0.02
Pupal width (mm)					
	Female	12.5 \pm 0.5	12.8 \pm 0.5	1.61	0.23
Male	10.2 \pm 0.3	10.4 \pm 0.7	0.51	0.49	
% female pupae	1	40 \pm 7	48 \pm 15	1.32	0.28

¹ Δ and \diamond indicate data square root and log transformed, respectively, for statistical analysis.

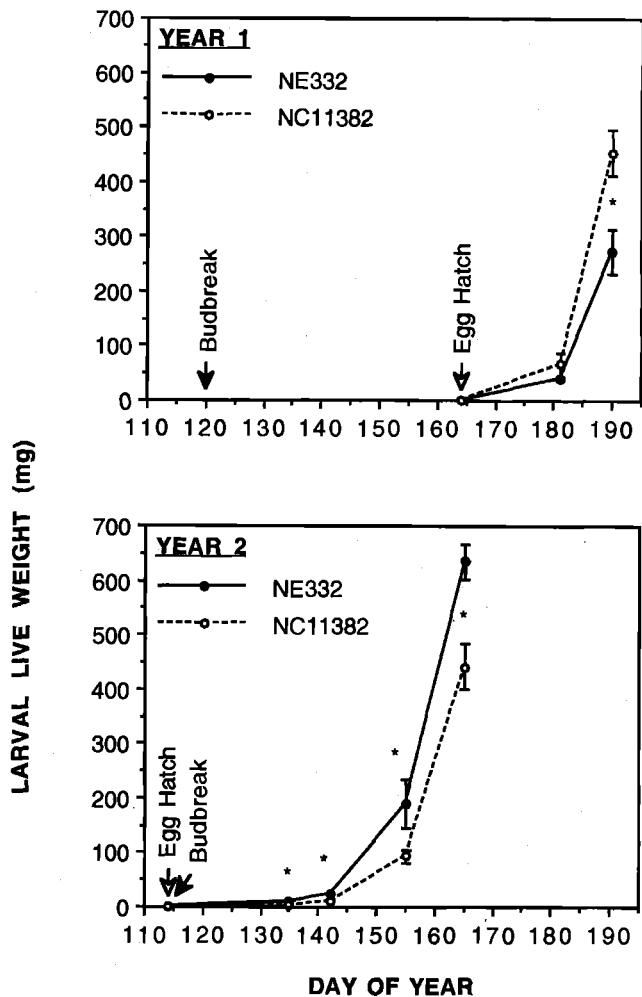


Figure 6. Larval growth ($\pm s_x$) on 2 hybrid poplar clones during 2 consecutive years, in whole-tree field cages. In Year 1 egg hatch was not synchronous with poplar spring budbreak, in Year 2 egg hatch and budbreak were in natural synchrony. * indicates significant differences between clones at each larval weight measurement, at the $P = 0.05$ level.

Oviposition by insect herbivores may not necessarily reflect plant suitability (Thompson and Pellmyr 1991). Although forest tent caterpillar ovipositional preferences among host species (Hodson 1941) and within native aspen clones

have been observed, such preferences have not been found among novel hybrid poplars that vary markedly in host quality (Robison and Raffa 1994). The absence of a correlation between oviposition site and food quality among novel hosts increases the importance of larval food choice and dispersal. Larval plant selection was correlated with larval development (Table 2, Robison 1993).

Coordinated movements of L1-L3 forest tent caterpillar colonies are affected by the quality and distribution of food plants. In mixed-tree plantings, colonies spent more time on the highly suitable host NC11004 than on the poor quality host NM6 (Table 3). However, colonies in uniform blocks did not readily move between clones, even though the preferred clones were only 23 cm away. This suggests that the effective area of food searching for young larvae is small, and that long-distance olfaction and vision are not major factors in food choice. This conclusion is supported by preliminary assays in which larvae did not respond to leaf odors in olfactometer tubes (Robison 1993).

Food evaluation appears to be based on sample feeding. For example, larvae in petri dish assays circle the dish and sample choices before prolonged feeding. We have also observed colonies moving within glasshouse and field trees prior to consuming all directly adjacent foliage. Similarly, late-instar forest tent caterpillars have been observed walking from partly defoliated native aspens into an adjacent hybrid poplar plantation. These observations suggest that differences among plants and leaves, and perhaps changes in foliar suitability within trees, affect larval behavior.

In choice tests among leaf positions within constitutive whole-plants, larvae generally preferred position Nos. 2–8 on clones NC11004, NC11382, NE332, and NM6 (Figure 3). In petri dish assays, larvae preferred positions 2 to 6 and 4 to 6 on clones NC11382 and NE332, respectively (Figure 2). Gypsy moths, *Lymantria dispar* (Meyer and Montgomery 1987), and cottonwood leaf beetles, *Chrysomela scripta* (Bingaman and Hart 1992, Harrell et al. 1982), also prefer these leaf positions. This suggests that similar foliar traits, such as phenolic compounds (Bingaman and Hart 1993, Lindroth 1992, Meyer and

Table 12. Stage-specific life table analysis of female forest tent caterpillars in whole-tree cages on hybrid poplar clones, averaged for 2 consecutive years; 100% egg band, egg, and pupal populations per cage (6 cages/clone); populations adjusted to females only for all life stages using percent female pupae in Year 1 for both years (NC11382 = 40%, NE332 = 48%).

Life stage (x)	No. alive at start of x (= l_x)	Mortality ¹ factor ($d_x F$)	No. dying during x (= d_x)	d_x as a % of l_x (= $100q_x$)
Clone NC11382				
Eggs	550.0	Nonviability	368.5	67.0
Larvae	181.5	Host plant effects	145.0	79.9
Pupae-adults	36.5	Nonviability	20.0	54.8
Ovipositing adults	16.5	—	—	—
Clone NE332				
Eggs	167.5	Nonviability	90.0	53.7
Larvae	77.5	Host plant effects	68.0	87.7
Pupae-adults	9.5	Nonviability	8.0	84.2
Ovipositing adults	1.5	—	—	—

¹ Egg nonviability due to infertility and natural enemies; larval parasitism measured only in Year 2 (parasitism on NC11382 = 2.4%, NE332 = 2.9%); pupal nonviability due to adult nonclosure, parasitism, and failure to oviposit.

Montgomery 1987), may be involved in feeding preference. Preferred feeding locations were less consistent on previously damaged than on constitutive plants (Figure 3). The data suggest that the preference for younger leaves on constitutive plants is lost on previously damaged plants. Furthermore, larvae may prefer older leaves on previously damaged plants (Figure 3). This change in feeding location between constitutive and previously damaged plants may result from higher levels of induction in leaf remnants among the preferred leaves on previously damaged plants, or be an artifact of the relative availability of leaves in different locations due to prior feeding.

Prior herbivory on hybrid poplars substantially affected subsequent forest tent caterpillar behavior and development. Constitutive trees were preferable to, and supported greater larval growth and survival than, previously damaged trees of the same clones (Tables 6–8). Both directly and systemically damaged foliage of clones NC11382, NE332, and NC11445 were induced (Table 6). These findings support the short-term foliar induction model of poplars described by Clausen et al. (1989).

The amount of directly damaged leaf induction was greatest in NC11445, intermediate in NE332, and least in NC11382 (Table 6). However, the intensity of induction in systemically damaged leaves did not vary among clones. These results suggest that relative levels of constitutive resistance (Table 2, Robison and Raffa 1994) are not necessarily correlated with inducibility, and that differences in inducibility among clones may vary among leaf conditions. However, choice tests between clones indicated that differences in constitutive suitability between clones were greater than the changes in suitability due to herbivory (Table 6). There were no significant differences in the intensity of feeding preferences between systemically and directly damaged leaves from clones NC11382, NE332, or NC11445 (Table 6).

Percent moisture, nitrogen, and fiber content (ADF or NDF) of constitutive leaves (Table 9) were not significantly correlated with clonal suitability (Table 2, Robison and Raffa 1994). However, percent nitrogen and moisture decreased, and fiber and toughness increased, in previously damaged relative to constitutive plants. These changes could potentially reduce the suitability of plants for folivores, and generally agree with the findings for nitrogen, moisture, fiber, and toughness of constitutive and previously damaged trees in other studies (Wagner 1988).

Extracts of poplar foliage elicited feeding responses (Table 10) similar to those found with excised and intact leaf tissues (Tables 4, 6–7, Robison and Raffa 1994). The constitutive NC11382 polar extract was preferred to the constitutive NE332 polar extract (Table 10). However, larvae tended to prefer the constitutive nonpolar extract of NE332 over NC11382 (Table 10). Both polar and nonpolar constitutive extracts from clones NC11382 and NE332 were preferred over extracts from previously damaged foliage (Table 10). Insect responses to nonpolar compounds in poplars have not been widely studied.

Polar extracts contain phenolics, including phenolic glycosides, which are known to vary among poplar species, clones, and leaves (Bingaman and Hart 1992, 1993, Lindroth 1992, Palo 1984, Ramachandran et al. 1994), affect insects (Bryant et al. 1987, Lindroth et al. 1986, Meyer and Montgomery 1987, Palo 1984), and increase following artificial defoliation (Clausen et al. 1989, Mattson and Palmer 1988). Hence, these compounds may have contributed to declines in plant suitability (Tables 6–8) or alterations in leaf position preference (Figure 3), following herbivory. However, little is known about the nonpolar components of poplar foliage that affect insects (Palo 1984). In preliminary chemical analyses of the constitutive polar and nonpolar foliar extracts used in the current study, no consistent relationships between the weight of extractable materials, the number of HPLC peaks, or the total height of HPLC peaks, and clonal suitability for the forest tent caterpillar were found (Table 2, Robison and Raffa 1994, Robison 1993). However, polar extracts from previously damaged foliage of clones NC11382 and NE332 yielded greater amounts of extractables, and number and total height of HPLC peaks, than did constitutive plants. Nonpolar extracts from previously damaged and constitutive NC11382 and NE332 had similar extractable weight and number of HPLC peaks, but total HPLC peak height was higher in the previously damaged trees.

The effects of plant traits on forest tent caterpillar behavior and development are manifested at the population level. In field cages, populations grew 12× larger on clone NC11382 than on NE332 in 2 yr (Table 11). Larval survival and adult viability were the first and second most important determinants of population change, respectively (Table 12). Although laboratory and glasshouse studies predicted that NC11382 would be a better host than NE332 (Robison and Raffa 1994, Robison 1993), field population responses were more complex, due to the effects of differing bud development (Figure 6). When larvae from artificially applied eggs in Year 1 fed immediately on fully expanded and preferred leaf positions, as in the laboratory studies, they developed faster, were heavier, and had greater survival on NC11382 than on NE332 (Table 11, Figure 6). However, when egg hatch (DoY 114) and spring budbreak (DoY 115; 343°C days > 0°C since DoY 1) were in natural synchrony on both clones in Year 2 (Robison 1993), development was faster on NE332 (Figure 6). Larval development on both clones was more rapid in Year 1 than Year 2 (Figure 6), probably due to warmer temperatures later in the season when eggs hatched in Year 1.

Resinous exudates on the buds and emerging foliage of NC11382, but not on NE332, prevented movement and feeding (Table 1). Curtis and Lersten (1974) had similar findings with cottonwood leaf beetle on *P. deltoides*. Thus, larvae on NC11382 did not feed until mature (drier) foliage developed, whereas larvae on NE332 began to feed immediately upon hatching and became developmentally advanced in Year 2 (Figure 6). Chemical differences between bud exudates of NC11382 and NE332 (Robison 1993) may have

also influenced larval feeding responses. Because 1st-instar larvae move and initiate feeding based on surface traits, quantities of extracts are more meaningfully expressed on a bud length (surface), rather than weight, basis. Buds may be somewhat stickier in the glasshouse than the field (Table 1) due to the drying effects of wind.

In the forest, larvae are known to remain on unopened buds for up to 3 wk (Lugger 1898), although they may suffer developmentally (Eggen 1978). In the field cages, larvae hatched before new NC11382 foliage was available and sufficiently dry for feeding, in the spring of Year 2. First-instar caterpillars appear to wait until foliage is available, and then after sample feeding may disperse in greater numbers from less suitable hosts. Waiting itself does not necessarily lead to dispersal losses. In both years sample feeding on NE332 revealed nonpreferred plant chemistry unrelated to bud conditions, and led to dispersal (see Table 2). However, larvae on NE332 that did feed in Year 2 became developmentally more advanced than larvae on NC11382, which had to wait for dry foliage to develop.

Despite differences in larval development among clones and years in the field cages (Figure 6), pupal size in Year 1 and fecundity in both years were equivalent on both clones (Table 11). Thus, insects which did survive achieved similar success on both clones. Similarly, pupal size was equivalent for insects reared on NC11382 and NE332 in laboratory assays (Robison and Raffa 1994). Egg viability and sex ratio were also equivalent on both clones in the field cages (Table 11). Thus, differences in population growth between the clones were not attributable to host effects on development rate (Figure 6), fecundity, or egg viability (Table 11). Rather, population change may have been governed primarily by larval survival, which was affected by allelochemicals (Ramachandran et al. 1994, Robison 1993), dispersal losses (Table 2), and interactions between development rate and survival (Figure 6, Robison and Raffa 1994).

The relationships between feeding ecology and population dynamics of the forest tent caterpillar among hybrid poplar clones are varied and complex. Interactions among foliar quality, availability, and responses to herbivory affect larval behavior, nutrition, and survival. The extent of foliar induction due to herbivory varies among genetically distinct clones. Larval responses to foliar characteristics exert both positive and negative feedback on herbivore success. Insect arrestment leads to increased group size and silk deposition, both enhancing larval performance. However, feeding elicits chemical alterations that both reduce larval success and elicit dispersal. Dispersal may occur between and within plants as leaf suitability changes. In addition to foliar properties that directly affect larval success, bud resins can also affect access to foliage. Thus scaling from controlled laboratory assays to whole-plant and population interpretations requires that direct and indirect interactions be considered. These interactions and relationships may partially explain forest tent caterpillar population cycles. They can also provide guidance to the development of heritable pest resistance in clones, and pest management strategies.

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